Climates past, present, and yet-to-come shape climate change vulnerabilities

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Abstract

Climate change is altering life at multiple scales, from genes to ecosystems. Predicting the vulnerability of populations to climate change is critical to mitigate negative impacts. Here, we suggest that regional patterns of spatial and temporal climatic variation scaled to the traits of an organism can predict where and why populations are most vulnerable to climate change. Specifically, historical climatic variation affects the sensitivity and response capacity of populations to climate change by shaping traits and genetic variation in those traits. Present and future climatic variation can affect both climate change exposure and population responses. We provide seven predictions of how climatic variation might affect the vulnerability of populations to climate change and suggest key directions for future research.

Keywords: adaptive capacity; climate change; climatic variation; sensitivity; spatial variation; temporal variation

Climatic Variation and Vulnerability

Climate change is altering all aspects of biological systems, from genes to ecosystems [1]. By 2100, climate change could cause the extinction of one in six species, alter the abundance and distribution of most that remain, and generate novel ecological communities [2, 3]. These changes will fundamentally alter life and have large impacts on human wellbeing [4]. Identifying which populations will be most vulnerable (see Glossary) to climate change has therefore become a major focus of ecology and evolutionary biology.

Climate change vulnerability depends on a population's exposure to climate change, sensitivity to abiotic and biotic changes, and ability to respond to those changes (i.e., response capacity) (Fig. 1) [5, 6]. A population's response capacity depends on factors such as genetic variation in traits affecting fitness and dispersal ability (intrinsic response capacity) as well as environmental factors such as dispersal barriers that influence climate change responses (extrinsic response capacity) [5, 6].

Here, we present a framework outlining how spatial and temporal variation in climate and weather (i.e., climatic variation) are key factors affecting each of these vulnerability components (Fig. 1). We follow previous research that defines temporal variation in relation to the resolution of an organism's generation time and spatial variation to the resolution of the area inhabited by a population (Box 1) [7, 8]. Defining temporal and spatial climatic variation in this way is consistent with the population-level responses that often underlie responses to environmental change, although other resolutions could be important (Boxes 1 and 4).

We suggest that historical variation in weather and climate has shaped the sensitivity and intrinsic response capacity of different populations and species to climate change by driving trait evolution and trait variation within and among populations (Fig. 1). Present and future variation in weather and climate will affect exposure and extrinsic response capacity (Fig. 1). Given that climatic variation differs around the globe, estimating regional climatic variation and interpreting this variation from an organismal perspective (Box 1) should help predict where and why populations will be vulnerable to climate change (Fig. 1).

We present seven testable predictions of how the sensitivity and response capacity of populations will differ between regions with high and low spatial or temporal climatic variation (Fig. 2). We then suggest future research directions to test these predictions and summarize the types of climates where populations are likely to be most at risk from climate change.

The Ghosts of Climate Past

Prediction 1: Populations from climates with high temporal or spatial variation will maintain higher genetic diversity, which increases their intrinsic response capacity.

When an environment varies in time or space, different genotypes can be favored at different times or locations. This varying selection can maintain high genetic variation in fitness despite stabilizing selection acting to reduce genetic variation [9]. Populations from climates with historically high temporal or spatial variation could therefore maintain higher additive genetic variation in fitness that allows them to evolve adaptations to climate change, increasing their intrinsic response capacity (Fig. 2A).

Temporal environmental variation that occurs among generations can preserve genetic variation by favoring different traits at different times and preventing one genotype from dominating a population [10-12]. This process is especially effective for long-lived species or species with propagule banks because old individuals or seeds can be less affected by episodic natural selection and therefore persist in the population despite many generations experiencing different selective optima [10, 11, 13]. For example, interannual temperature variation maintains genetic variation in silver birch (*Betula pendula*) stands by favoring recruitment of different genotypes in different years [10]. This genetic variation could facilitate evolutionary adaptation to climate change over the next 33-55 years [10]. Also, seasonal temperature variation maintained genetic variation in *Drosophila subobscura* that facilitated a rapid evolutionary response to a recent heat wave [14].

Theory suggests that spatial climatic variation within and among populations can maintain more genetic variation than temporal variation [9] by mixing individuals adapted to different local conditions [15, 16]. For instance, genetic variation in lodgepole pine (*Pinus contorta*) is higher in regions with higher spatial climatic variation [17]. This mechanism requires that gene flow is sufficient to spread alleles within and among populations, but not enough to prevent local adaptation [17-19]. In addition to increasing additive genetic variation [17], spatial climatic variation can provide a source for individuals pre-adapted to future climates [20, 21]. For instance, warm-adapted genotypes might move to higher altitude sites, displacing cold-adapted genotypes as they go [20, 21].

Populations that occur in temporally variable climates might not have higher genetic variation if they can avoid local weather extremes, for example by moving among microclimates within an area. Also, genetic variation in small isolated populations, such as those that occur on mountaintops, could remain low despite high temporal and spatial climatic variation [22]. Whether genetic variation will allow populations to evolve fast enough to persist under climate change depends on factors such as the amount of future climatic variation, rate of climate change, generation time, and the persistence of maladapted individuals (see Prediction 6; [23-25]). Evolution might also be slowed by phenotypic plasticity [26], which can evolve under climatic variation (see Prediction 2). Theory suggests, however, that plasticity is more likely to facilitate than hinder evolution under climate change by buffering populations from declines and providing extra time for evolutionary responses [26].

Prediction 2: Populations from climates with high temporal variation will have higher phenotypic variation increasing their intrinsic response capacity.

Genotypes within populations often vary their phenotype to cope with high temporal variation in weather that occurs either within or among generations. Two different strategies of phenotypic variation have evolved depending on the predictability of climatic variation (Box 2): phenotypic plasticity and bet hedging. Both could increase a population's intrinsic response capacity.

In climates with high temporal variation that is predictable via a cue (e.g., seasonal temperature variation predicted via day length), populations typically evolve adaptive phenotypic plasticity [27, 28]. Changes in physiology and the timing of flowering or migration are common examples. If environmental cues remain reliable under climate change, plasticity could increase the intrinsic response capacity of populations by allowing phenotypic adjustments to climate change [26, 29]. Indeed, many populations have already adjusted the timing of key events (e.g., migration) and traits (e.g., body size) in response to recent climate change [29]. Such plastic responses might not be enough for population persistence, but could allow time for other climate change responses to become effective (e.g., evolutionary adaptation [30, 31]). However, plasticity will only increase a population's intrinsic response capacity if the cue remains reliable and the phenotype generated under novel climates remains adaptive [26, 32].

In climates with high temporal variation that is unpredictable (e.g., interannual rainfall in arid regions; Box 2) populations often evolve diversified bet-hedging strategies, where individuals produce offspring with different phenotypes or oviposit in different microclimates to spread their risk in unknown future conditions [27, 28, 33]. These strategies reduce the long-term variance in fitness, which increases population persistence in a variable environment even though population mean fitness might be reduced. Bet hedging could increase a population's intrinsic response capacity by reducing the fitness costs of unfavorable future conditions and allowing time for other climate change responses such as climate tracking and evolution. Bet hedging is likely to be especially effective in the short-term when environments vary between novel and historical conditions. However, bet hedging will only increase intrinsic response capacity if the costs (e.g., seed bank mortality) remain sufficiently low under future climates [34].

Prediction 3: Populations from climates with low spatial or high temporal variation will evolve higher dispersal propensity, which increases their intrinsic response capacity.

Dispersal is risky in spatially variable climates with low autocorrelation (Box 2) because a disperser is likely to encounter unsuitable climates (Fig. 2C) [35, 36]. Remaining in a location with unpredictable temporal variation (Box 2) is also risky because the current location could become unsuitable in the future [36, 37]. Consequently, populations from locations with low spatial climatic variation or high temporal climatic variation often evolve higher dispersal propensity [36-38].

Higher dispersal propensity can allow populations to track suitable climates under climate change. For example, European dragonflies from standing freshwater systems have higher dispersal propensity than those from running freshwater systems because running systems are more ephemeral on long-time scales, although other explanations exist [39]. The higher dispersal propensity of dragonflies from running systems allowed them to recolonize central Europe after the last glaciation [39], occupy a greater portion of suitable habitat [40], and track contemporary climate change better than species from standing systems [41].

The evolution of dispersal propensity depends on many other factors such as the need to avoid inbreeding or competition [37]. However, spatial and temporal environmental variation is a key factor that could predict the dispersal propensity [37] and therefore the intrinsic response capacity of many populations.

Prediction 4: Populations from climates with high temporal variation among generations will evolve broad thermal tolerances that decrease their sensitivity to climate change.

Seventy years ago, Scholander et al. observed that endotherms have a broader thermal neutral zone in the arctic than the tropics [42]. Two decades later, Janzen suggested that temperate ectotherms evolved broader thermal tolerances than tropical ectotherms in response to greater temperature seasonality in temperate regions [43]. Recent studies confirm these patterns [44, 45] and demonstrate a clear link between thermal tolerance breadth and seasonal temperature variation (Box 1 and 3; [46, 47]).

Evolved differences in thermal neutral zones and tolerances due to seasonal temperature variation (Box 3) strongly affect climate change sensitivity (Fig. 2D) [44, 48-50]. Populations with broader thermal tolerances are less likely to experience heat stress under climate change [44, 48, 50]. Also, species with broader thermal tolerances often have larger geographical ranges [47, 51], which can reduce their vulnerability to climate change because their range is more likely to incorporate low vulnerability regions (e.g., low exposure, fewer dispersal barriers) [52, 53]. Therefore, temperate organisms are often predicted to be less vulnerable to climate change than tropical organisms, despite higher predicted increases in temperature in temperate versus tropical regions [44, 48, 54].

These predictions depend on a few key assumptions [55-57]. Predictive models must represent future temperature variation accurately, convert environmental temperature to body temperature, and allow for negative intrinsic population growth rates to make accurate future predictions of vulnerability [49, 50, 55, 57-59]. Models with these assumptions often predict that species in the subtropics are most vulnerable to climate change because they live closer to their upper thermal limit (Box 3), but experience relatively high temperature variation [50, 58]. Although, fitness losses in the subtropics could be moderated by lengthening growing seasons [58]. In addition, fitness measured at constant temperatures or for short periods, as is customary when measuring thermal tolerances, might not predict fitness under variable temperatures or under prolonged exposure [60, 61]. Organisms might also regulate their temperature behaviorally (e.g., by moving among microclimates), which would limit their vulnerability to climate change [55, 57, 62]. However, these behaviors often come with high costs such as reduced foraging time, which can negate their benefits [63]. Despite these caveats, the relationship between temporal temperature variation and thermal tolerances should indicate which populations are most sensitive to climate change.

Extrinsic Response capacity under Climates Present and Yet-to-Come

Prediction 5: Climate tracking will be more effective in climates with high spatial variation, which increases the extrinsic response capacity of populations.

Climate can differ dramatically over short distances due to factors such as topography, shading, and proximity to large water bodies [64]. For example, temperature differences over a few meters in a forest canopy can mimic those observed over hundreds of meters in elevation or many kilometers in latitude [38]. In contrast, climates might be similar across hundreds of meters in other landscapes.

Spatial climatic variation will affect a population's extrinsic response capacity by affecting how populations track suitable climates. Populations in locations with little variation will often need to move long distances to track suitable climates (Fig. 2E) making them more vulnerable to climate change [65]. Conversely, high spatial climatic variation could facilitate climate tracking in several ways. Populations might only need to move short distances to track suitable climates or avoid extreme weather events (Fig. 2E) [65, 66]. Patches of suitable climate could also act as stepping stones through unsuitable areas or microrefugia where populations could persist for many decades [64, 67, 68]. Many populations are thought to have persisted in such microrefugia throughout past climate changes [69-71], and many studies suggest that microrefugia will be critical for population persistence under future climate change [72-74].

High spatial climatic variation can also allow small populations to persist outside the more contiguous species' range. These populations can expand when the surrounding climate becomes suitable, increasing range expansion rates from those predicted based on homogeneous environments [71, 75, 76]. This mode of climate tracking could explain how trees quickly refilled their ranges during post-glacial climate warming in North America and Europe [71, 75].

Spatial variation might also hinder climate tracking under some circumstances. Unsuitable climates can act as dispersal barriers, especially for species with narrow climatic tolerances [43, 77]. High spatial climatic variation can also increase the likelihood that passive dispersers settle in unsuitable locations [35].

Prediction 6: Populations will track suitable climates more slowly in climates with high temporal variation, which decreases their extrinsic response capacity.

In climates with high temporal variation, weather during a relatively short period (e.g., days, weeks, decades) can differ substantially from the long-term trend. For example, February 2015 in the northeastern USA was the second coldest on record despite a 3.9 °C increase in average February temperature since 1900 [78].

Periods that deviate from the long-term trend can slow climate tracking if climates along range-shift pathways become temporarily unsuitable [76, 79-81] or by eliminating populations colonizing regions that recently became suitable (Fig. 2F) [82-84]. For example, amphibians in the western USA might not track suitable climates because decadal climate fluctuations cause gaps between areas where climate is currently suitable and areas predicted to be suitable in the future [79]. Also, a short cold snap in winter 2010 lead to range retractions of exotic species that had previously expanded their range from the Caribbean into the USA [82]. Decreased climate tracking rates can increase extinction risk under climate change [79, 81], especially for populations and life-stages that are sensitive to short-term climate fluctuations [79, 84].

Prediction 7: Evolutionary adaptation of populations will lag further behind long-term climate change in regions with high temporal variation, thereby decreasing the extrinsic response capacity of populations.

Theoretically, a population can evolve adaptations in response to current and future climate change provided the rate of climate change does not exceed a critical rate, which depends on generation time, maximum population growth rate, genetic variation in fitness, and the strength of selection [24, 25]. In addition, current and future temporal environmental variation among generations can reduce the rate of climate change a population can adapt to, decreasing a population's extrinsic response capacity (Fig. 2G).

Temporal climatic variation among generations can cause adaptations to climate in one time period to be maladaptive in subsequent time periods as the environment varies [24]. This maladaptation can cause demographic and genetic bottlenecks that slow adaptation rates by removing standing genetic variation [24]. The rate of environmental change a population can adapt to is less affected if temporal variation is autocorrelated (Box 2) because evolution in one time period is less likely to be maladaptive in subsequent time periods [85]. Recent predictions of the evolution of wing melanin in alpine and subalpine butterflies demonstrate how temporal variation in weather can slow evolutionary adaptation to climate change [86]. Temperature variation has caused variation in the direction (for or against wing melanin) and the magnitude of selection, resulting in very little directional evolution under recent climate change, despite directional changes in temperature.

Under some circumstances, however, high climatic variation can aid evolutionary adaptation. For instance, extreme weather events can remove maladapted adults of long-lived organisms, which can facilitate the recruitment of better-adapted individuals [87].

Testing Predictions is the Next Step

Many studies forecast climate change responses for particular populations or regions, but rarely test their predictions using data from the responses of populations to recent climate change or climate change experiments. An important next step is to test the predictions presented here using climate change experiments and comparative analyses of climate change responses (e.g., distribution and phenological changes) among regions with climates that differ in the magnitude of temporal and spatial climatic variation. Data on responses to recent climate change is now available in many regions to facilitate these tests. We provide four recommendations on how to test the predictions reviewed here.

1. Few studies evaluate how climatic variation at local scales affects the sensitivity and response capacity of populations. If populations are adapted to local climatic variation, then maps of spatial and temporal variation combined with knowledge of how populations are adapted to such variation could make fine-scaled predictions about the vulnerability of populations to climate change, rather than being limited to broader generalizations such as tropical versus temperate regions. We suggest comparing traits (e.g., thermal tolerance breadth) and climate change responses among populations that

occur in a similar region but experience different amounts of climatic variation (e.g., forest floor versus canopy [38]). Such studies would help determine the spatial scale at which the seven predictions presented here are valid and how this varies depending on the life history of the organisms concerned (Box 1).

2. We need to understand how spatial and temporal climatic variation interacts to affect climate change vulnerability (Box 4). A mosaic of climates with different combinations of spatial and temporal variation occurs across the globe (Fig. 1C). In many cases, spatial and temporal variation have opposing effects on a population's vulnerability, and we do not understand which will dominate. Studies that compare the responses of species to climate change among areas with similar temporal variation but different spatial variation (or vice versa) will be necessary to understand how spatial and temporal variation interact to affect climate change responses.
3. We advocate for more realistic predictive models that incorporate climate data at relevant resolutions and aspects of biology sensitive to climatic variation (Boxes 1 and 4) [88]. Although suitable climate data might not yet be available for all circumstances [7, 89], biologists are increasingly gaining access to climate data with finer spatial and temporal resolutions (e.g., [64]). These models will facilitate more accurate predictions of climate change impacts that better inform policy decisions.
4. The population-level predictions reviewed here should be expanded to understand vulnerability in communities of interacting species. Such an approach requires understanding both the filtering of species by traits and the evolution of their

populations to climates and other species. The evolving metacommunity framework provides one such approach to understanding this complexity [90].

Where Might Populations be Most Vulnerable

Given the seven predictions presented here, populations living in places with high spatial climatic variation (e.g., mountainous regions, Fig. 1) should be less vulnerable to climate change owing to a higher response capacity (Fig. 2). These populations often maintain higher genetic variation, and although they might disperse less, they should also track suitable climates more easily. Small populations currently restricted to isolated mountaintops are likely an exception. By contrast, species living in climates with less spatial variation (e.g., inland plains) could have lower standing genetic variation, and their higher dispersal propensity might act only to compensate for the farther distances they must travel to find future suitable climates.

The effects of temporal climatic variation are less clear because temporal variation affects sensitivity and response capacity in conflicting ways. Populations experiencing more temporal variation could be less sensitive to climate change and maintain more genetic variation in traits related to climate change resilience, but encounter interruptions to climate tracking and evolution that increase extirpation risk and reduce genetic variation. Conversely, populations experiencing less temporal climatic variation could be more sensitive to climate change and have less genetic variation, but ecological and evolutionary responses might be more consistent and effective. Resolving these conflicting effects on sensitivity and response capacity will require targeted experiments and models.

Concluding Remarks

Few studies incorporate spatial or temporal variation into experimental designs or predictive modeling. Here, we stress that past, present, and future climatic variation are important ecological and evolutionary forces that shape the sensitivity and response capacity of populations under climate change. Indeed, the predictions we present here are only a subset of the ways in which climatic variation affects vulnerability. Appreciating the significance of climatic variation will significantly improve our understanding and predictions of where and why populations will be vulnerable to climate change.

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Figure Legends

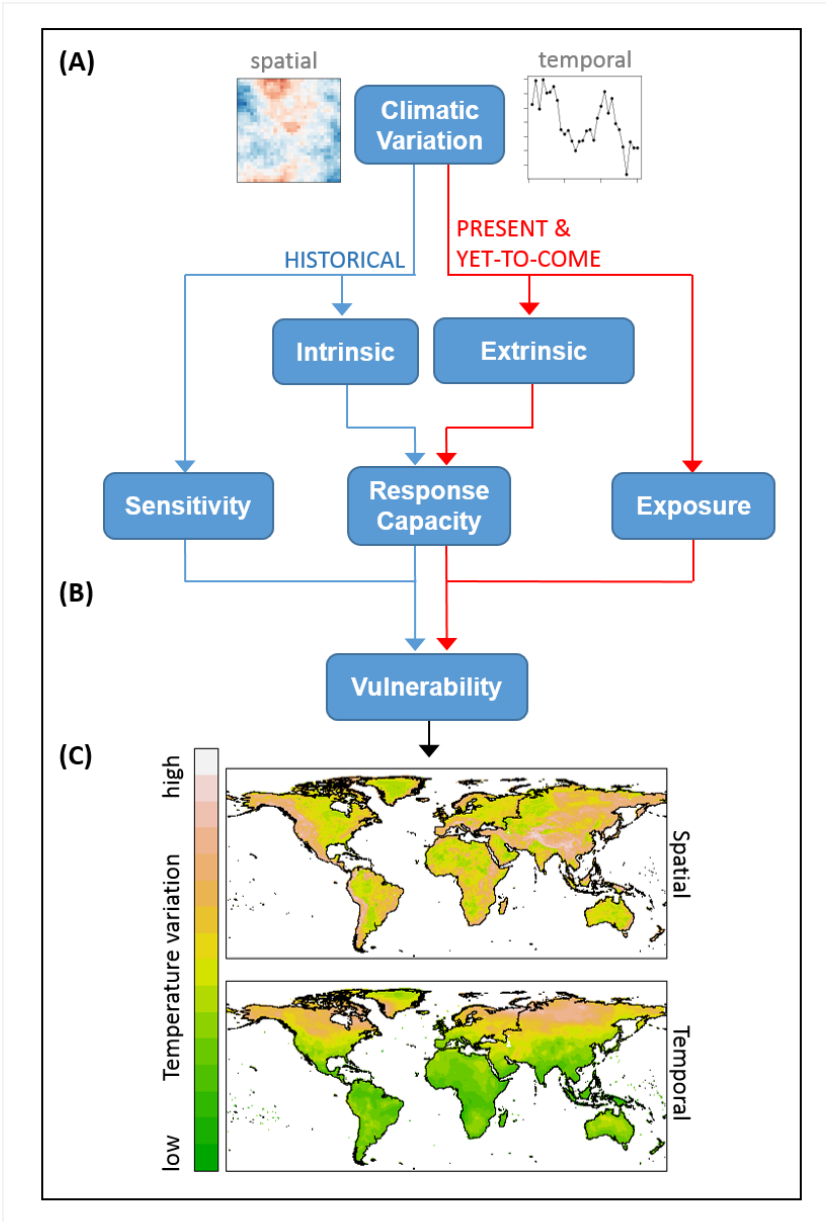

Figure 1. A conceptual model of how spatial and temporal climatic variation predict the vulnerability of populations to climate change. (A) Spatial and temporal climatic variation affect the exposure, sensitivity, and response capacity of populations under climate change. Historical climatic variation affects the intrinsic response capacity and sensitivity of populations, and

present and future climatic variation affect the exposure and extrinsic response capacity. (B) Exposure, sensitivity, and response capacity are key components determining the vulnerability of populations to climate change. (C) Given that climatic variation differs around the globe, maps of climatic variation scaled to the traits of the focal population (e.g., dispersal ability, generation time; Box 1) can predict where and why populations will be most vulnerable to climate change. The upper map shows current spatial variation within 31 by 31 km pixels and was produced using climate data with a 1 km resolution [91]. The lower map shows interannual variation in temperature between 1900 and 2010 based on Climatic Research Unit TS 3.23 data [92].

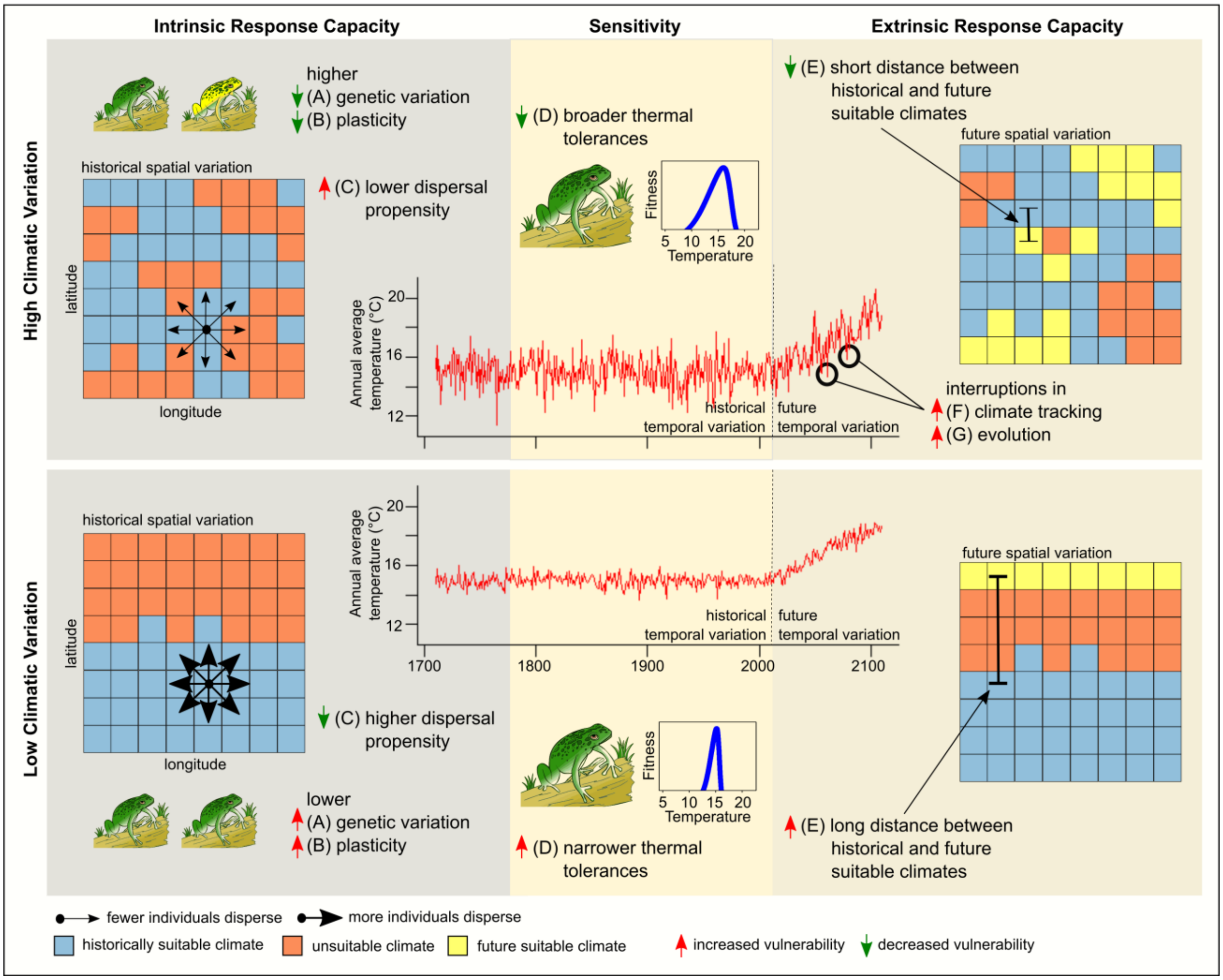

Figure 2. Seven potential differences in the sensitivity, intrinsic response capacity, and extrinsic response capacity of populations from locations with high or low spatial and temporal climatic variation. Effects on vulnerability are shown with the colored arrows. Historical spatial and temporal variation can maintain higher (A) genetic variation (see Prediction 1) and (B) plasticity (see Prediction 2), increasing the intrinsic response capacity of a population. (C) Historical spatial variation can decrease dispersal propensity, decreasing the intrinsic response capacity of a population (see Prediction 3). (D) Historical temporal variation can increase thermal tolerance breadth, decreasing the sensitivity of a population (see Prediction 4). (E) The distance between current and future suitable climates is shorter in climates with high spatial climatic variation,

increasing the extrinsic response capacity of a population (see Prediction 5). Present and future temporal variation can cause interruptions in (F) climate tracking (see Prediction 6) and (G) evolution (see Prediction 7), decreasing the extrinsic response capacity of a population.

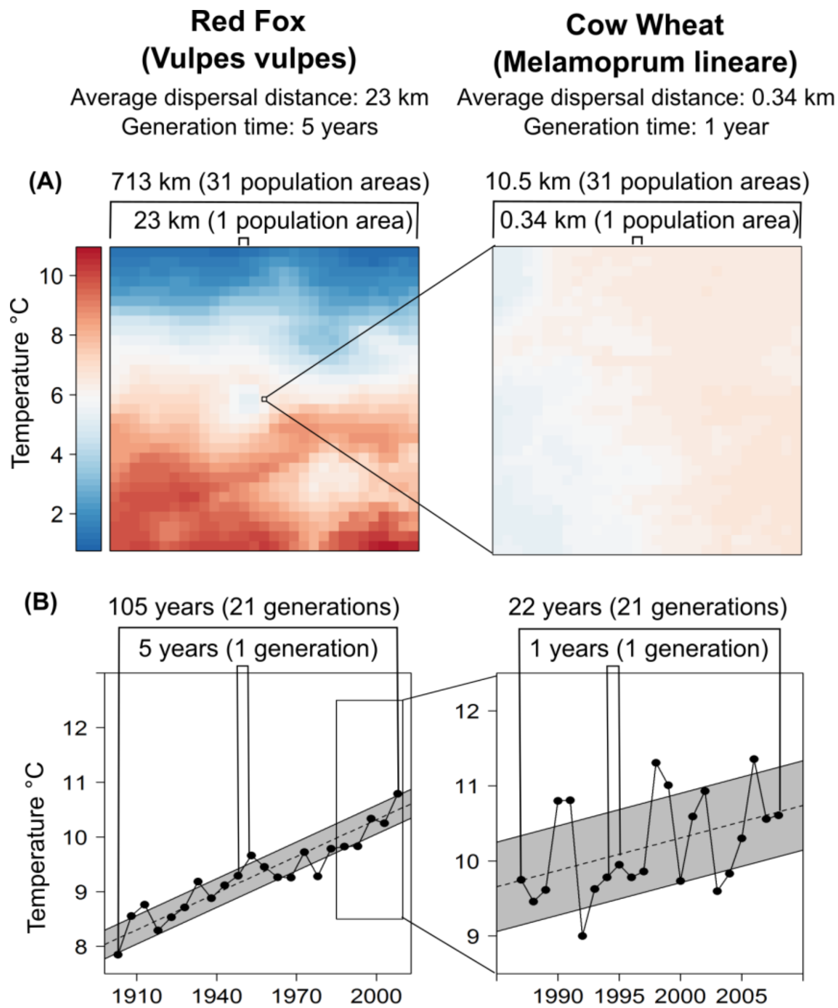

Figure I. Examples of (A) spatial and (B) temporal climatic variation for species with different dispersal abilities and generation times. We scaled the spatial resolution (i.e., the grid cell area) to be the area inhabited by a population for each species, which we define as the area encompassing 86.5% of dispersal events (i.e., Wright's dispersal neighborhood; [7, 15]). We scaled the study area to include 15 population areas in each cardinal direction from the center cell. We scaled the temporal resolution to one generation and the focal time period to include 21 generations. Scaling the study area, focal time period, and resolution of the climate data in this way demonstrates how species with different dispersal abilities and generation times might experience climatic variation differently. The red fox will experience more spatial climatic variation in its study area, but cow wheat will experience more temporal temperature variation among generations in the focal time period. This figure is modified from ref [7].

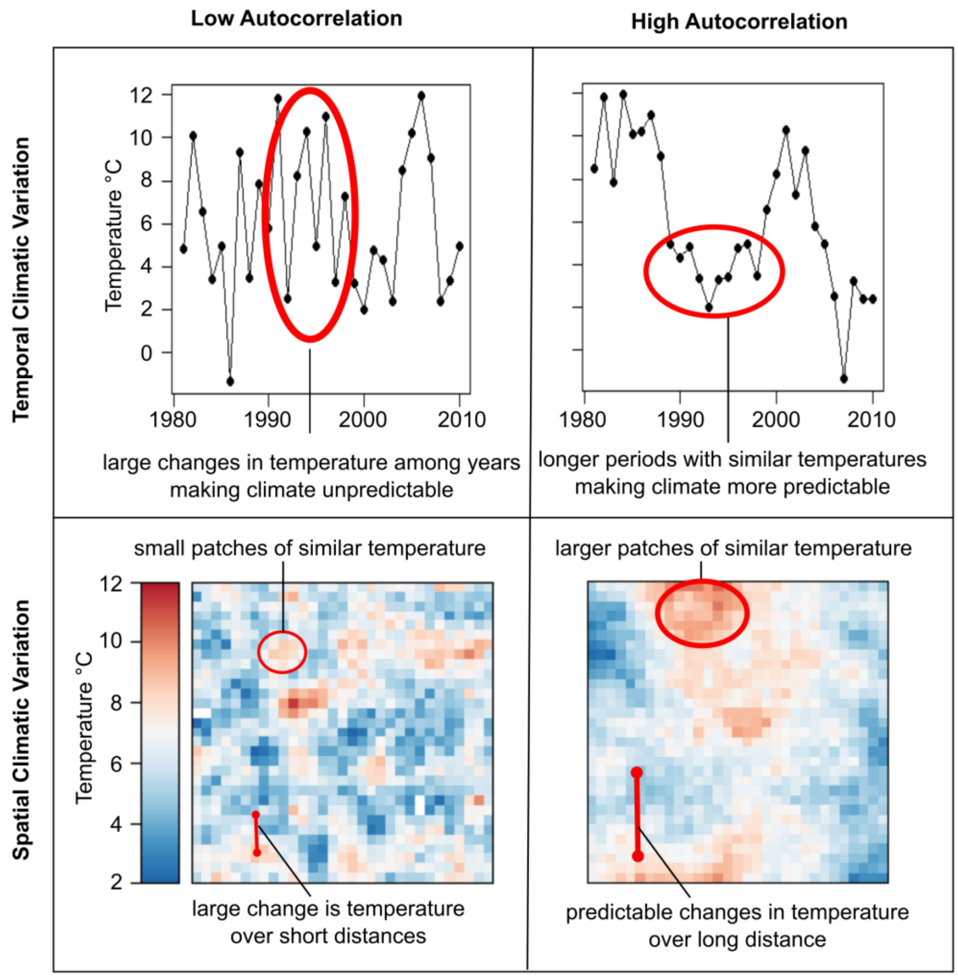

Figure II. Examples of spatial and temporal climatic variation with different amounts of autocorrelation. Climatic variation with higher autocorrelation has longer time periods or larger distances with similar climates, which makes climate more predictable over time and space.

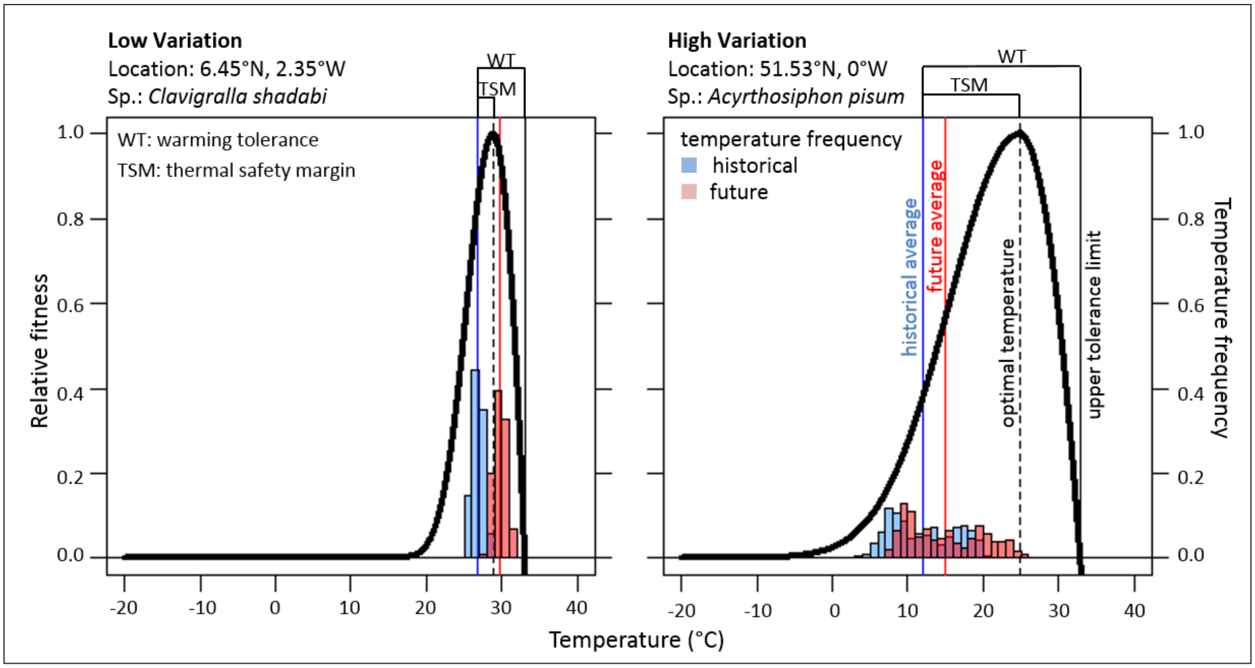

Figure III. Thermal performance curves (thick black line) from two true bug (Hemiptera) populations that occur in climates with low (left) and high (right) temporal variation in temperature. Historical (blue), future (red), and overlapping (purple) temperature variation is shown in the histograms, and averages are shown with the colored vertical lines. The optimal temperature is shown with the dashed line and the upper tolerance limit is shown with the thin black line. The current thermal safety margin (TSM) and warming tolerance (WT) are shown above each plot. Populations from more variable climates have larger thermal safety margins and warming tolerances, which makes them less sensitive to climate change. Temperature data was obtained from the National Center for Atmospheric Research model [93] forced under Resource Concentration Pathway 8.5. This figure is modified from [48].

Box 1: An Organismal Perspective on Climatic Variation

Climates and weather vary on multiple spatial and temporal scales ranging from millimeters and minutes to kilometers and millennia. Organisms experience this variation differently depending on their life history and behaviors. Researchers must consider how the focal organism experiences climatic variation to make accurate predictions of climate change responses. Here we highlight three key aspects of this organismal perspective.

Life History and Behavior

Organisms experience climatic variation differently depending on their life history and behavior [59]. For example, a species might have a particularly sensitive life stage [59, 84] or avoid extreme weather through behaviors such as hibernation or by utilizing particular microclimates [57, 59]. To accurately predict climate change responses, it is crucial to focus on the most sensitive life stages, model important behaviors, and filter climate data to include only those time periods when a species is active.

Biological Scaling of Climate Data

Accurately predicting climate change responses requires scaling climate data to the organism and process under investigation [7, 94]. Fig. I shows how scaling of the study area, focal time period, and resolution of climate data might differ between two species with different dispersal abilities and generation times. These scaling differences affect how the organisms experience spatial and temporal climatic variation. For example, the red fox (*Vulpes vulpes*) will experience more spatial climatic variation within the study area (Fig. IA), but cow wheat (*Melampyrum lineare*) will experience greater temporal temperature variation among generations (Fig. IB).

Most climate change impact assessments do not scale climate data based on the biology of focal species [7, 89], which likely reduces predictive accuracy [79, 81, 95, 96]. More research is needed to determine how best to scale climate data to accurately represent climatic variation in climate change vulnerability assessments (Box 4).

Effects of Different Resolutions

Climatic variation at different resolutions can have opposing effects on the same population. For instance, when temperature varies within generations, populations often evolve narrow thermal tolerances and concentrate their activity during times when temperatures are suitable [47, 97]. However, this strategy could be maladaptive when temperatures vary among generations because temperatures might never be suitable during the lifetime of future offspring. Thus, populations evolve broad thermal tolerances to cope with temperatures that vary among generations [47, 97]. More research is needed to determine the effect of climatic variation at different resolutions and how variation at different resolutions interacts to affect species' traits (Box 4).

Box 2. Biological Effects of Climatic Autocorrelation and Predictability

Here, we focus primarily on the magnitude of climatic variation, contrasting locations with high and low variation (Fig. 2). However, the autocorrelation and predictability of climatic variation are also important.

Autocorrelation describes the similarity between neighboring measurements of weather or climate in time or space (Fig. II). If climatic variation is positively autocorrelated, then the conditions in one time period or location will be similar to conditions in neighboring time periods or locations (Fig. I). Positively autocorrelated climates have longer time periods of similar weather or larger areas of similar climate (Fig. I). Climatic variation that is positively autocorrelated is also predictable because the weather or climate in the current time period or location is likely to be similar in neighboring time periods or locations (Fig. I). Climatic variation can also be predictable from external cues such as day length or tidal variation.

Autocorrelation and predictability of historical climatic variation has had strong biological effects. For example, populations evolve phenotypic plasticity when historical weather is predictable because phenotypic adjustments to match the current weather conditions are likely to be adaptive in future time periods [27, 28]. However, if conditions vary unpredictably, then phenotypic adjustments in response to current weather are unlikely to be adaptive under future conditions. Therefore, when weather varies unpredictably, populations evolve bet-hedging strategies such as variation in the duration of dormancy in seed banks of desert plants [27, 28, 33, 34]. The autocorrelation of historical climatic variation can also affect the evolution of dispersal propensity (see Prediction 3).

The effect of autocorrelation in current and future climatic variation has received less attention, but is likely to be an important factor in predicting climate change responses. For example, one of the few studies that focused on current temporal autocorrelation demonstrated how sustained warm periods in a climate that is temporally autocorrelated can allow a warm-adapted species to shift its distribution under climate change by providing a sustained competitive advantage over resident species [98]. Temporal autocorrelation can also affect evolution to changing climates by affecting the rate of evolution (see Prediction 7), and the fate of beneficial mutations [99]. Presumably, spatial autocorrelation will also affect the ability of species to track suitable climates by affecting the size of climatically suitable patches and the size of climatic dispersal barriers [35, 79]. Such effects of spatial autocorrelation on the responses of species to climate change require more detailed research.

Box 3. Temperature Variation and Climate Change Sensitivity

Organisms from climates with higher temperature seasonality often have broader thermal tolerances [42-45], but do not necessarily have higher thermal maxima (cf. upper limits in Fig. III). In fact, upper thermal tolerances vary little within and among species across broad temperature gradients [45]. So, why might organisms from climates with high temperature seasonality be less sensitive to climate change?

The answer is due, in part, to the commonly observed steep decline in fitness at warmer temperatures, which makes it costly to experience temperatures warmer than the optimum (Fig. III). Under variable temperatures, an organism maximizes long-term fitness by living in a location that is cooler on average than the optimal temperature (Fig. III). This reduces the likelihood of experiencing temperatures warmer than the optimum, which would cause severe fitness declines (Fig. III). As temperature variation increases, the difference between the average temperature where an organism occurs and the optimal temperature (i.e., thermal safety margin) [48] also increases (Fig. III). Large thermal safety margins can buffer increases in average temperature due to climate change by decreasing climate change sensitivity (Fig. III) [48].

In addition, organisms that occur in cooler climates often have an increased buffering capacity because there is a bigger difference between the average environmental temperature where they occur and their upper thermal tolerance limit (i.e., warming tolerance; Fig. III) [48]. Climates with high temporal temperature variation often occur at northern latitudes where average temperatures are also cooler. Consequently, organisms that occur in cool, variable climates also tend to have a greater warming tolerance (Fig. III) [48]. This additional buffering capacity in climates with high temperature seasonality further decreases climate change sensitivity [48].

Lastly, organisms that occur in locations with higher temperature seasonality can often shift their phenology to cope with increasing temperatures. Indeed, the projected vulnerability of temperate organisms to climate change decreased substantially when models allowed for phenological responses to climate change [48, 58]. In fact, increasing temperatures will lengthen the active season for many ectotherms living in cooler climates, which could increase long-term fitness [48, 58]. By contrast, phenological shifts are less likely to help populations in locations with little temperature seasonality because shifts in activity time will not correspond to large temperature changes.

Box 4. Outstanding Questions

- What is the ideal spatial and temporal resolution of climate data to predict the response of a population to climate change? Which traits determine the ideal resolution? Debate exists on the climate data resolution necessary to accurately predict climate change vulnerability [7, 8, 89]. Few studies have attempted to determine the ideal resolution and how that might differ among species (but see [95]). Recent responses of populations to climate change could be used to help determine what climate data resolution best explains observed climate change responses.

- How does climatic variation at different resolutions interact to affect climate change vulnerability? Climatic variation at different resolutions can have opposing effects on the vulnerability of populations to climate change (Box 1). However, we know little about how these resolutions interact to affect climate change vulnerability. Experiments and models that expose populations to climatic variation at multiple resolutions will be necessary to address this issue.
- How do spatial and temporal climatic variation interact to affect climate change vulnerability? Spatial and temporal variation can have opposing effects on the vulnerability of populations to climate change (Box 1). Global climates are composed of many combinations of spatial and temporal variation (Fig. 1C). It is therefore critical to resolve how different combinations of spatial and temporal variation will interact to affect climate change vulnerability.
- How will changes in spatial and temporal climatic variation affect climate change vulnerability? Climatic variation is likely to change in the future [100]. The literature reviewed here demonstrates that climatic variation affects many aspects of biology. Thus, changes in climatic variation and its predictability will likely affect climate change

vulnerability. Future studies need to accurately account for potential changes in climatic variation to better predict climate change responses.

Glossary

Additive Genetic Variation: the portion of phenotypic variance among individuals that is due to the average effects of alleles across many genotypes and not due to dominance or epistasis. Additive genetic variation determines the potential for evolutionary responses.

Exposure: the amount of climate change experienced by an individual or population in the absence of any response (e.g., movements, changes in phenology) to that change [5].

Extrinsic response capacity: the component of response capacity determined by factors external to an individual or population [5]. These factors constrain the intrinsic response capacity during the response. For example, dispersal barriers can limit the ability of a population to track suitable climates, decreasing its extrinsic response capacity.

Intrinsic response capacity: the component of response capacity determined by individual and population-level traits (e.g., dispersal ability, genetic variation in phenology). For example, a population with high dispersal propensity will be better able to track suitable climates and will therefore have a higher intrinsic response capacity.

Microrefugia: small areas relative to the traits of the focal species or population where microclimates or microclimate variation buffers populations against climate change [64].

Phenotypic Plasticity: the degree to which a single genotype expresses different phenotypes in response to changes in the environment. Phenotypic changes can occur in the lifetime of an individual (i.e., reversible plasticity) or be fixed during development (i.e., irreversible plasticity).

Response capacity: the ability of an organism, population, or species to mitigate the adverse effects of climate change [5] by tracking suitable habitats, evolutionary adaptation, or phenotypic plasticity. Response capacity is commonly referred to as adaptive capacity [5], but here we use the term response capacity to reduce confusion with the narrower evolutionary definition of adaptive capacity. Response capacity can be partitioned into two components: intrinsic and extrinsic response capacity.

Sensitivity: the degree to which climate change will adversely affect the fitness of an individual or population that does not respond to changing climates [5]. Sensitivity quantifies the fact that the same change in climate will not affect all organisms equally.

Thermal Neutral Zone: the temperature range within which an endotherm's rate of heat production is in equilibrium with the rate of heat loss to the environment. Outside of this zone an endotherm must expend energy to thermoregulate.

Vulnerability: the propensity to be adversely affected by climate change, including (but not limited to) decreases in abundance, loss of genetic variation, extirpation, and extinction [5]. Vulnerability is often partitioned into three components: exposure, sensitivity, and response capacity.

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